

THE COMPARATIVE MORPHOLOGY OF THE WINTERACEAE III. WOOD

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With four plates

GÖPPERT (22) in 1842 noted the absence of vessels in the wood of *Drimys Winteri* J. R. and G. Forst. His observations have been verified by Eichler (18), Möller (29), De Bary (17), Solereder (34, 35), Strasburger (36), Groppler (23), and many other anatomists and taxonomists. That *Trochodendron* has a similar vesselless type of wood was reported by Eichler (18) in 1864. *Tetracentron* was subsequently added to the list by Harms (24) in 1897. It was upon the basis of their vesselless wood that van Tieghem (38) segregated the genera *Drimys*, *Pseudowintera*,¹ *Bubbia*, *Belliolum*, *Exospermum*, *Zygogynum*, *Trochodendron*, and *Tetracentron* in three families of a distinct order, the Homoxylées. Thompson and Bailey (37) and Bailey and Thompson (9) studied all organs and parts of *Drimys Winteri* J. R. & G. Forst., *Pseudowintera axillaris* var. *colorata* (Raoul) A. C. Sm., *Trochodendron*, and *Tetracentron*, and demonstrated that vessels and vessel-like structures are absent throughout both the primary and secondary bodies of these plants.

In assembling all available collections of Winteraceae for taxonomic revision, my colleague Dr. Smith (32, 33) has provided me with the unusual opportunity of studying the anatomy of a wide range of accurately identified representatives of the family. Vessels are invariably absent from both the primary and the secondary xylem. Parmentier (30) obviously erred in reporting the presence of vessels in two putative species of *Drimys*. As van Tieghem (38) and others have shown, Parmentier's observations were based upon incorrectly determined material. Thus, increasing evidence accumulated by many investigators during the last 100 years indicates that the Winteraceae (excluding *Illicium*), *Trochodendron*, and *Tetracentron* are the only known living representatives of the dicotyledons that have a primitive vesselless type of secondary xylem. This is not indicative necessarily of close genetic relationship between the Winteraceae, *Trochodendron*, and *Tetracentron*, as assumed by van Tieghem, but rather the occurrences are to be regarded as retentions of a primitive ranalian type of wood by three families which exhibit diverse trends of specialization in their other vegetative characters and in their reproductive organs.

During the last 25 years, the study of the comparative anatomy of the cambium and xylem has progressed rapidly to a stage where it is possible to visualize the salient trends of evolutionary specialization of these tissues

¹*Pseudowintera* Dandy, i.e. *Wintera* sensu v. Tiegh., non Murray.

in the gymnosperms and angiosperms. Particularly in the case of the cambium (2, 3, 4), vessels (6, 10, 16, 19, 20, 21), imperforate tracheary cells (7, 10), and rays (8, 12, 13, 14, 27) of dicotyledons, the irreversible trends of structural specializations are so obvious and clearly defined that they may be utilized, even statistically, in evaluating the levels of morphological specialization that have been attained within specific groups of plants (6, 7, 8, 25, 26, 39, 40).

The cambium of the Winteraceae, as of *Trochodendron* and *Tetracentron*, is of the same cytological and histological type as that which occurs so characteristically in the lower vascular plants which form vesselless secondary xylem. The fusiform initials of the non-stratified cambium periodically divide diagonally, elongate extensively, and commonly attain lengths of as much as 5000 microns in the outer parts of old stems. Since the changes in length and tangential diameter of the tracheary derivatives are relatively slight during tissue differentiation, the tracheids of the Winteraceae resemble the fusiform initials in length and tangential outline and tend to be arranged in relatively undisturbed radial seriations, *Figs. 1-3* and *7-9*. The primitive character of the cambium and xylem in the Winteraceae, *Trochodendron*, and *Tetracentron* rules out any possibility of these plants having developed vessels and subsequently having lost them. Wherever vessels have originated (primary body of *Selaginella*, *Pteridium*, and monocotyledons, secondary body of Gnetales and dicotyledons), their development is closely correlated with fundamentally significant cytological, histological, and ontogenetic changes in the xylem. In the case of the dicotyledons, which have now been very comprehensively investigated, the development and the specialization of vessels is closely synchronized with significant changes in the cambium and xylem. Furthermore, it should be emphasized in this connection that in those dicotyledons (e.g. Cactaceae, Crassulaceae, aquatics, and other super-specialized forms) where there is a tendency towards the reduction or elimination of vessels, the tissues are obviously profoundly modified and highly specialized. There is no evidence of reversible transitions leading toward a reversion to the primitive type of cambium and xylem that characterizes the Winteraceae, *Trochodendron*, *Tetracentron*, and the lower vascular plants.

In the past, many investigators have referred to the wood of *Drimys* as having a coniferous type of structure. Such comparisons between the Winteraceae and the Coniferae are misleading, since they overlook outstanding structural differences. The wood rays of the Winteraceae, *Trochodendron*, and *Tetracentron* are of the primitive heterogeneous type I (Barghoorn, 12) that characterizes the secondary xylem of anatomically less specialized dicotyledons. Two widths of rays occur typically in this form of ray structure: (a) uniseriates and (b) multiseriates. The uniseriate rays which extend outward from the fascicular parts of the stele are composed of vertically much elongated cells, whereas the multiseriate rays which extend outward from the gaps in the stele are constituted of more nearly isodiametric or radially elongated cells, *Figs. 1-6*. Both

types of rays increase in number in enlarging stems by appropriate cytological changes in the cambium (Barghoorn, 12); both are much extended longitudinally in the first formed secondary xylem and are dissected into lower rays during subsequent enlargement of the stem. In the Cordaitales, Ginkgoales, and Coniferae, not only are there no multiseriate rays comparable to those of the dicotyledons, but also the characteristically uniseriate (occasionally bi- or tri-seriate) rays are of a basically different type. The coniferous uniseriate ray is very low in the first-formed secondary xylem and commonly increases in height during subsequent enlargement of the stem (Barghoorn, 11). Furthermore, it is composed usually of radially rather than vertically elongated cells. Mixtures of narrow and wide rays do occur, however, in the wood of the Pteridospermae, Bennettiales, and Cycadales, and the wood of Pteridospermae frequently exhibits a heterogeneous type of ray structure (Andrews, 1).

The tracheary pitting in the primary xylem of *Ginkgo*, the Coniferae, and the Gnetales is of a highly modified type (Bailey, 5) and is entirely unlike that which characterizes the lower vascular plants and the angiosperms. Furthermore, the scalariform and transitional types of tracheary pitting in the secondary xylem of the Winteraceae, *Trochodendron*, and *Tetracentron* have no counterparts among the Cordaitales, Ginkgoales, Coniferae, or Gnetales, but closely resemble those types that occur in the secondary xylem of certain Bennettiales and *Protopitys*. Thus, if the vesselless wood of the Winteraceae is to be compared with that of the gymnosperms, it should be with the secondary xylem of Pteridospermae and Bennettiales rather than with that of the Coniferae, Ginkgoales, or Cordaitales.

The wood parenchyma, tracheids, and rays of the Winteraceae fluctuate considerably in available samples of the wood of different representatives of the family, *Figs. 1-8, 10, and 11*. Thus the woods of the New Caledonian *Zygogynum Vieillardii* Baill., *Figs. 1 and 4*, the Solomon Island *Belliolum haplopus* (Burt) A. C. Sm., *Figs. 3 and 6*, and the Chilean *Drimys Winteri* J. R. and G. Forst., *Figs. 2 and 5*, are composed of much larger tracheids than those of the Australian *Drimys lanceolata* (Poir.) Baill., *Figs. 7 and 10*, and the New Zealand *Pseudowintera axillaris* var. *colorata* (Raoul) A. C. Sm., *Figs. 8 and 11*. Growth rings, *Fig. 7*, are well developed in the sample of *Drimys lanceolata* but are not detectable in the other illustrated specimens. Wood parenchyma, which is absent or of infrequent occurrence in *Drimys Winteri*, *Fig. 2*, is more or less abundantly developed in the other woods and exhibits diffuse, diffuse-in-aggregates, and tangentially banded distributions. The multiseriate rays vary in height and width, in the size and form of their constituent cells, and in their number within a unit area, *Figs. 1-8, 10, and 11*. The uniseriate rays fluctuate in height and in the vertical extension of their constituent cells. The character of the tracheary pitting also varies considerably, the ratios of scalariform to multiseriate-circular to uniseriate-circular fluctuating from specimen to specimen.

It has been customary in the past to utilize such differences in the construction of keys for differentiating the woods of genera and species. There is, however, a very considerable element of uncertainty in so doing, unless unusually extensive collections of each species are available. This is due to the fact that the structural characters enumerated in the preceding paragraph commonly fluctuate more or less markedly, not only within different parts of the same tree, but also in trees grown under different environmental conditions. Furthermore, it is difficult at present to determine from herbarium specimens (twigs) what the expression of diagnostic characters in the outer parts of large stems will be. Therefore, any deductions regarding generic differences between the woods of the Winteraceae are tentative and subject to future verification. Available material suggests that there are at least two significant trends of structural specialization within the Winteraceae, one leading toward a marked reduction in the amount of wood parenchyma in the New World *Wintera* section of *Drimys*, and the other toward a reduction in cell size and a striking enlargement of the multiseriate rays in *Pseudowintera*.

The vesselless woods of *Trochodendron* (Japan and Formosa) and *Tetracentron* (Central China) are characterized by their conspicuous annual growth rings, *Fig. 9*. In fact, the growth rings are as contrastedly developed as those of *Keteleeria*, *Larix*, and other conifers of the northern hemisphere. The tracheids of the earlywood are large, thin-walled, and provided with scalariform bordered pitting such as occurs so generally in the tracheids of ferns. On the contrary, those of the latewood are smaller, thick-walled, and have scattered small circular bordered pits. The tracheids of the transitional region exhibit transitions between scalariform and multiseriate-opposite, multiseriate-alternate, and uniseriate-circular types of pitting, such as occur in the Winteraceae and certain Bennettitales (Bailey and Thompson, 9). The ray structure is conspicuously heterogeneous as in the Winteraceae, but the multiseriate rays (in wood from large stems) are lower, are composed of smaller cells, and have a fusiform outline in tangential sections, *Fig. 12*. Diffuse parenchyma is confined largely to the latewood, *Fig. 9*. Thus, the vesselless wood of *Trochodendron* and *Tetracentron* differs from that of the Winteraceae in its conspicuous growth layers, in the dominantly scalariform pitting of its earlywood, and in its specialized form of heterogeneous ray structure. The question arises how significant are such structural differences in considering possible relationships within the Ranales.

Growth rings in trees are commonly interpreted as being conditioned by environmental influences. There are, however, two distinct types of zonation phenomena in wood: (1) facultative and (2) obligate. Many tropical and subtropical plants as well as plants of the southern hemisphere form growth rings or not, depending upon the environment in which they are grown. The growth rings of certain Winteraceae, *Fig. 7*, as of many Podocarpaceae and Araucariaceae appear to be of this facultative type. On the contrary, many plants of the northern hemisphere form zonate wood

under all conditions of survival, both natural and experimental. The growth rings of *Trochodendron* and *Tetracentron*, with their associated characteristic type of tracheary pitting, appear to be of the obligate type. Thus, fossilized representatives of these genera from the Jurassic (?) of India (Sahne, 31), the Tertiary of northwestern United States (Beck, 15), and the Eocene of Greenland (Mathiesen, 28) have wood that is indistinguishable structurally from that of the postglacial living representatives.

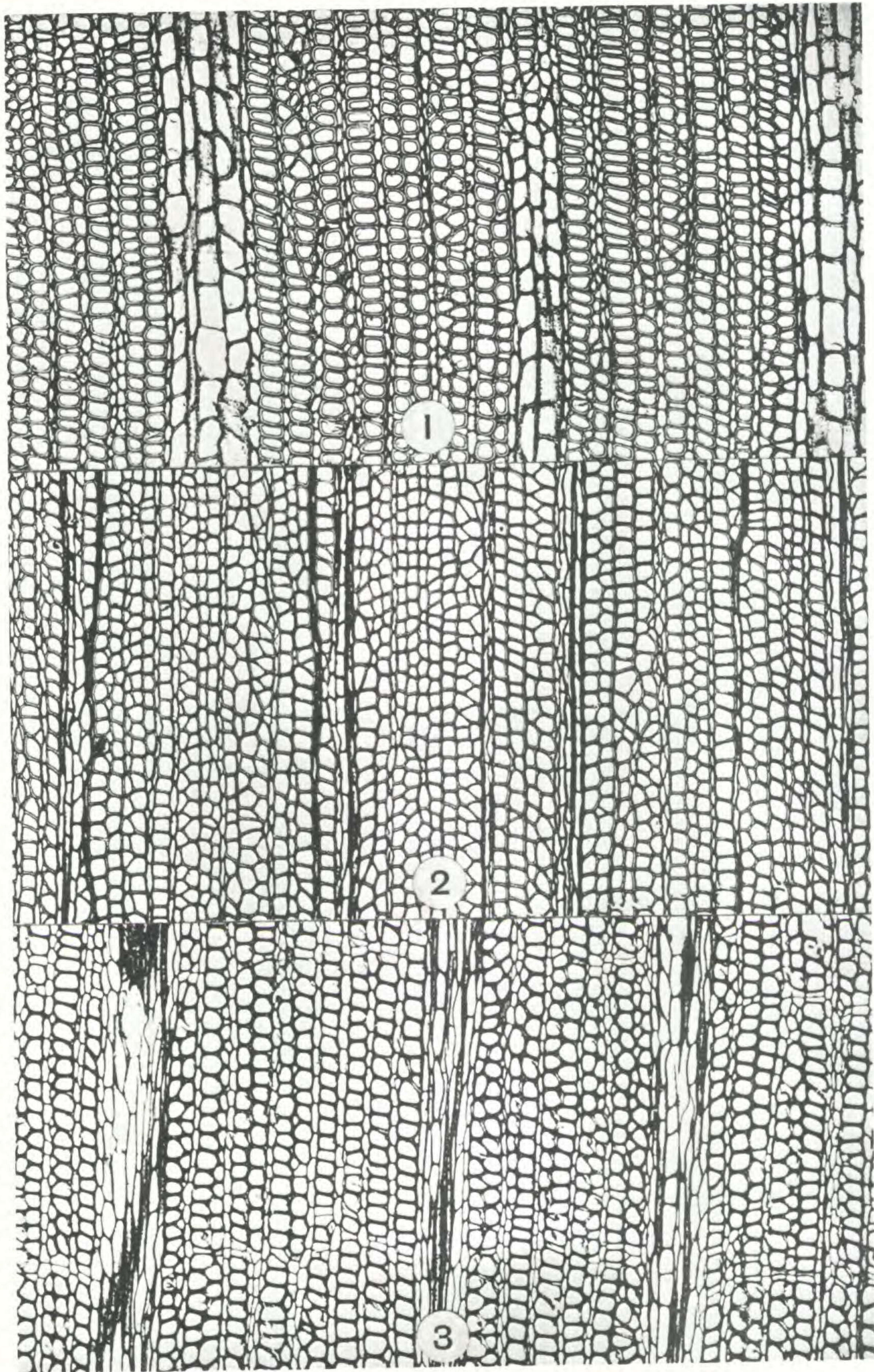
From the point of view of the comparative anatomy of the vascular plants as a whole, the obligate growth layers of *Trochodendron* and *Tetracentron* and the segregation of scalariform pitting in excessively thin-walled earlywood tracheids are evidence of structural specialization. The type of ray structure illustrated in *Fig. 12* arises in other dicotyledonous families as specializations from such ray forms as occur in the Winteraceae. This suggests that the wood of the Winteraceae is of a more primitive and plastic ranalian type, resembling that from which the modified and stereotyped wood of *Trochodendron* and *Tetracentron* has been derived. It should be noted in this connection that in young stems of Winteraceae (Bailey and Thompson, 9), as in the wood of certain Bennettitales, the scalariform tracheids tend to be segregated in the earlywood when unusually conspicuous growth layers are developed.

It is unlikely that the dicotyledonous type of vessel could have originated in a specialized vesselless wood of the trochodendraceous type, since the more primitive types of vessels in dicotyledons are diffused throughout the wood and are not in zonal arrangements. Although the plastic vesselless wood of the Winteraceae more closely approximates the type in which vessels originated, the actual ancestral forms must have contained a higher ratio of scalariform pitting than occurs in most living representatives of the Winteraceae, which exhibit evidences of reduction in the amount of such pitting. When the summation of evidence from all organs and parts of the plants is taken into consideration, there are no convincing arguments for deriving the Trochodendraceae from the Winteraceae or vice versa or even for inferring that these families are closely related genetically. Nor can one assume that other ranalian families were derived from these specific vesselless families. Each of the latter exhibits a combination of more or less primitive and specialized characters, indicative of reticulate rather than linear relationships and of common origin from an ancestral ranalian stock. Until essential fossilized material is discovered, the composite structure of such ancestors can be synthesized only by combining the more primitive features of a number of diverse families.

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